4. Dreyer, G., Ray, W., and Walker, E. W. Ainley, 1912, "The Size of the Aorta in certain Animals and its Relation to their Body Weight," 'Journ. Physiol.,' vol. 44, p. viii.
5. Meeh, K., 1879, "Oberflächenmessungen des menschlichen Körpers," 'Zeitschr. f. Biologie,' vol. 15, p. 425.
6. Keilson, Hermann, 1898, 'Beitrag zur Lehre von der Pulsfrequenz,' Dissert. Königsberg in Pr.
7. Thoma, R., 1882, 'Untersuchungen über die Grösse und das Gewicht der anatomischen Bestandtheile des menschlichen Körpers in gesunden und kranken Zustand,' Leipzig.

The Size of the Trachea in Warm-Blooded Animals, and its Relationship to the Weight, the Surface Area, the Blood Volume, and the Size of the Aorta.

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The analysis of data collected in connection with the investigation of a number of problems in immunity has led to a series of results, in part already published, bearing upon the blood and circulation. The conclusion was reached that in certain cases a precise and definite relationship to the body surface exists in warm-blooded animals in accordance with the formula $W^n/a = k$, where W is the body weight of the animal, a represents the mass of the body fluid, tissue, or organ under investigation, k is a constant, and the value of n is approximately 0·70–0·72.

In view of the fact that the carriage of oxygen is one of the chief functions of the circulation, and that the volume of the blood (1), (2), and the aortic area (3), (4), (area of cross-section of aorta), have been shown by us to be proportional to the body surface in warm-blooded animals, while, as we have also found, the total oxygen capacity is the main factor in determining the size of the heart (5), it appeared to be of interest to examine the size of the channel by which the oxygen gains access to the lungs.

Accordingly, the trachea was measured in two species of mammal and one bird, namely, guinea-pig, rabbit, and ptarmigan. The animals used were healthy individuals in good condition, not previously experimented upon,

and many of them were made use of at the same time for measuring the size of the aorta. The guinea-pigs and rabbits had all been kept in the laboratory under as equable conditions as possible as regards food, etc. Pregnant animals were, of course, excluded. The ptarmigan were purchased from a game dealer, and were carefully selected.

Methods.—The technique employed was identical with that described in a previous paper (4) for the determination of the size of the aorta. The *internal* πr of the trachea was carefully measured at a point just above its bifurcation, and from this the radius and the sectional area were determined. As we have pointed out before (4), the method made use of is open to considerable experimental error, but this is greatly reduced by multiplying the number of individual observations of each trachea, and also diminishes greatly with increasing practice. The body weights recorded are the natural weights (in grammes) of the animals immediately before they were killed, and consequently include the weight of the contents of the alimentary canal.

Table I.—Guinea-pig (individuals).

No.	Sex.	Body weight.	Radius of trachea.	Area of tracheal cross-section.	$k = W^{0.72}/T$.	Tracheal cross-section as percentage of body weight.	Cross section calculated. $T = W^{0.72}/k$. ($k = 23 \cdot 4$.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (0·908) of body weight.	Difference between cross-section calculated and observed.
		grm.	mm.	sq. mm.				per cent.		per cent.
1	♂	70	0·605	1·06	20·1	1·52	0·91	16·5	0·635	67·0
2	♀	170	0·814	2·46	16·4	1·45	1·72	43·0	1·54	59·8
3	♂	220	0·745	1·74	28·0	0·791	2·08	16·3	2·0	13·0
4	♀	220	0·892	2·5	19·4	1·14	2·08	20·2	2·0	25·0
5	♂	230	0·742	1·73	29·0	0·753	2·15	19·5	2·19	21·0
6	♀	230	0·733	1·68	29·9	0·73	2·15	21·8	2·19	23·3
7	♂	300	0·796	1·99	30·4	0·664	2·58	22·8	2·72	26·8
8	♂	330	1·035	3·36	19·4	1·02	2·78	15·1	3·0	12·0
9	♀	360	1·031	3·34	20·7	0·928	2·96	12·8	3·27	2·14
10	♀	390	1·082	3·68	19·9	0·944	3·13	17·6	3·54	3·96
11	♀	410	1·157	4·2	18·1	1·02	3·24	29·6	3·72	12·9
12	♂	420	0·97	3·0	25·8	0·714	3·31	9·36	3·81	21·2
13	♂	490	0·988	3·06	28·3	0·625	3·79	17·3	4·45	31·2
14	♂	493	1·179	4·35	20·0	0·883	3·72	16·9	4·48	29·0
15	♀	620	1·115	3·90	26·2	0·629	4·37	10·7	5·63	30·8
16	♀	640	1·203	4·55	23·0	0·711	4·47	1·79	5·81	21·7
				Average	23·4	0·908	—	18·2	—	25·1

Observations.—In Table I are given the figures and calculations for 16 guinea-pigs, ranging in weight from 70 to 640 grm. (*i.e.* increasing more

than ninefold). From this table it is seen that, as would be expected, the tracheal area (sectional area of the trachea) increases much more slowly than the body weight, so that the *ratio* of the tracheal area to the body weight decreases steadily as the weight of the animal increases. But it appears on calculation that the body weight (W) to the nth power (where n is approximately 0·70–0·72) divided by the sectional area (T) is a constant (k).

This gives the formula $W^n/T = k$, which indicates that *the tracheal area (area of the cross-section of the trachea) is a simple function of the surface of the body*, since, as we have shown, the body surface may be determined accurately from the formula $S = k.W^n$ by taking n to be approximately 0·70–0·72 instead of $\frac{2}{3}$, as was done by Meeh (6).

Table I further shows that the average value of k is 23·4, corresponding to an n of 0·72, which is by calculation the best n for these observations, and that if the tracheal area be calculated from the formula $T = W^n/k$, using these values for n and k, the average percentage deviation of the observed from the calculated values is 18·2. If, on the other hand, the sectional area is expressed in percentage of body weight (0·908), the average deviation between the calculated and the observed values is 25·1 per cent.

It may be stated further that if the value 0·71 is taken for n, the average value of k becomes 21·5.

To bring out the various points more clearly, as well as to get rid of irregularities due to individual variations in the animals and to experimental errors, the animals have been grouped in Table II.

The guinea-pigs are arranged in five groups according to weight, and the

Table II.—Guinea-pig (grouped).

Group.	Numbers of individuals from Table I in group.	Average body weight.	Average radius of trachea.	Average area of tracheal cross-section.	$k = W^{0.71}/T$.	Tracheal cross-section as percentage of body weight.	Cross-section calculated. $T = W^{0.71}/k$. ($k = 21·3$.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (0·965) of body weight.	Difference between cross-section calculated and observed.
		grms.	mm.	sq. mm.				per cent.		per cent.
A	1	70	0·605	1·06	19·3	1·51	0·959	10·53	0·676	56·8
B	2–6	214	0·785	2·02	22·4	0·944	2·12	4·72	2·07	2·42
C	7–10	345	0·986	3·09	20·5	0·896	2·98	3·69	3·33	6·31
D	11–14	453	1·074	3·65	21·1	0·806	3·61	1·11	4·37	16·48
E	15–16	630	1·159	4·23	23·0	0·671	4·56	7·24	6·08	30·43
				Average	21·3	0·965	—	5·46	—	22·49

weights, the tracheal radii, and the tracheal areas of the animals in each group averaged. The other figures are calculated from these average values.

It is found that, under these circumstances, the best n is 0·71, and the average value of k is 21·3. Using these values for n and k, the average deviation between the calculated and the observed figures is 5·46 per cent., while it is 22·49 per cent. if the tracheal area (T) be calculated as a percentage (0·965) of body weight. If the value of n be taken as 0·70, k is 20·1, but, if n be taken as 0·72, k becomes 22·5, and the corresponding average percentage deviation is 5·76 instead of 5·46. If, however, the appropriate allowance be made for the number of individuals in each group, the percentage deviations become 4·22 (with $n = 0{\cdot}72$) and 4·24 (with $n = 0{\cdot}71$). So that the value 0·72 for n is in reality slightly better than 0·71, as it was in the case of the individual animals.

Further, it will be observed that, while the k exhibits no periodic variation as the weight of the animal increases, the tracheal percentage (tracheal area expressed in per cent. of body weight) decreases very greatly and with absolute regularity from 1·51 to 0·671.

Table III.—Rabbit (individuals).

No.	Sex.	Body weight.	Radius of trachea.	Area of tracheal cross-section.	$k = W^{0{\cdot}70}/T$.	Tracheal cross-section as percentage of body weight.	Cross-section calculated. $T = W^{0{\cdot}70}/k$. ($k = 12{\cdot}5$.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (0·83) of body weight.	Difference between cross-section calculated and observed.
		grm.	mm.	sq. mm.				per cent.		per cent.
1	♀	940	1·8	10·2	11·8	1·084	9·62	6·02	8·2	24·4
2	♀	970	1·76	9·69	12·8	1·001	9·92	2·32	8·47	14·4
3	♀	1100	1·88	11·1	12·2	1·009	10·8	2·78	9·6	15·62
4	♂	1330	1·96	12·06	12·8	0·906	12·3	1·95	11·62	3·79
5	♂	1420	2·09	13·8	11·6	0·972	12·8	7·82	12·4	11·3
6	♀	1600	2·23	15·6	11·2	0·975	14·0	11·4	13·97	11·67
7	♀	1880	2·1	14·0	14·0	0·745	15·7	10·8	16·41	14·7
8	♀	2040	2·45	18·9	11·0	0·927	16·4	13·9	17·82	6·06
9	♂	2080	2·22	15·4	13·6	0·74	16·8	8·34	18·15	14·6
10	♂	2180	2·26	16·1	13·1	0·739	17·4	7·47	19·03	15·39
11	♀	2280	2·42	18·4	12·1	0·807	17·9	2·79	19·9	7·54
12	♀	2750	2·58	20·8	12·3	0·76	20·4	2·45	24·0	12·9
13	♂	2970	2·54	20·3	13·3	0·684	21·5	5·58	25·92	21·68
				Average	12·5	0·873	—	6·43	—	13·39

Table III gives the figures and calculations for the tracheas of 13 rabbits (tame) ranging in weight from 940 grm. to 2970 grm. (*i.e.* increasing more

than threefold). The average tracheal constant (k) is 12·5 with an n of 0·70, which is the best n for these observations, and the average tracheal percentage is 0·873. It is seen that, as was the case in the guinea-pigs, the variations of the tracheal constant show no periodicity, but the tracheal percentage falls markedly, though not quite regularly (from 1·084 to 0·684). If the tracheal area (T) is calculated by our formula, the average deviation between the calculated and the observed figures is 6·43 per cent., while it is 13·39 per cent. (more than twice as great) when the area is calculated in per cent. of body weight. If the value 0·71 be taken for n, the value of k becomes 13·4.

Table IV.—Rabbit (grouped).

Group.	Numbers of individuals from Table III in group.	Average body weight.	Average radius of trachea.	Average area of tracheal cross-section.	$k = W^{0.70}/T$.	Tracheal cross-section as percentage of body-weight.	Cross-section calculated. $T = W^{0.70}/k$. ($k = 12·5$.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (0·880) of body-weight.	Difference between cross-section calculated and observed.
		grm.	mm.	sq. mm.				per cent.		per cent.
A	1—2	955	1·78	9·95	12·3	1·04	9·75	2·05	8·4	18·45
B	3—4	1215	1·92	11·58	12·5	0·953	11·54	0·35	10·69	8·33
C	5—7	1633	2·14	14·47	12·3	0·886	14·2	1·9	14·37	0·7
D	8—11	2145	2·34	17·2	12·5	0·802	17·18	0·12	18·88	8·9
E	12—13	2860	2·56	20·6	12·8	0·72	21·02	2·0	25·17	18·16
			Average		12·5	0·88	—	1·28	—	10·91

In Table IV the rabbits are arranged in the usual way in five groups. As in the case of the individual observations the best n is 0·70, giving an average k of 12·5. The variations in the tracheal constants (for the groups) are small and are non-periodic, while the tracheal percentage falls with absolute regularity from 1·04 in the lightest group to 0·72 in the heaviest group. Using the values just stated for n and k, the average percentage deviation of the observed from the calculated figures is 1·28, while it is 10·91 (more than eight and a-half times as large) if the area be calculated as a percentage of the body weight. If n is taken as 0·71, k becomes 13·4.

Table V gives the figures for the tracheas of 10 ptarmigan purchased from a game-dealer. They had been shot for the market, and exhibit the greatest range of weight that we were able to obtain, namely, from 460 grm. to 710 grm. The average tracheal constant (k) is 7·45 with an n (best n) of 0·71, and the average tracheal percentage is 2·16. The variations of the

Table V.—Ptarmigan (individuals)

No.	Sex.	Body weight.	Radius of trachea.	Area of tracheal cross-section.	$k = W^{0.71}/T$.	Tracheal cross-section as percentage of body-weight.	Cross-section calculated. $T = W^{0.71}/k$. ($k = 7{\cdot}45$.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (2·16) of body weight.	Difference between cross-section calculated and observed.
		grms.	mm.	sq. mm.				per cent.		per cent.
1	♀	460	1·81	10·33	7·6	2·25	10·54	1·99	9·94	3·92
2	♀	470	1·84	10·58	7·48	2·25	10·61	0·28	10·14	4·34
3	♀	500	1·81	10·33	7·98	2·06	11·09	6·85	10·8	4·35
4	♀	530	1·97	12·25	7·05	2·31	11·59	5·74	11·43	7·17
5	♀	538	1·96	12·12	7·15	2·27	11·62	4·3	11·62	4·3
5	♀	553	1·95	11·98	7·38	2·17	11·88	0·84	11·94	0·34
7	♀	590	2·01	12·63	7·33	2·14	12·42	1·69	12·73	0·79
8	♀	600	1·99	12·44	7·53	2·08	12·59	1·19	12·96	4·01
9	♀	630	2·04	13·03	7·46	2·07	13·05	0·15	13·6	4·19
10	♀	710	2·11	14·0	7·53	1·97	14·16	1·13	15·23	8·62
			Average		7·45	2·16	—	2·42	—	4·2

tracheal constant show no periodicity, but the tracheal percentage decreases steadily, although not regularly, from 2·25 in the lightest, to 1·97 in the heaviest animal. When the tracheal area (T) is calculated by our formula the average deviation of the observed from the calculated values is 2·42 per cent., while it is 4·2 per cent. (nearly twice as great) if the area be calculated in per cent. of body weight. If the value of n be taken as 0·70 k becomes 7·0, and if n be 0·72 k is 7·93.

Table VI.—Ptarmigan (grouped).

Group.	Numbers of individuals from Table V in group.	Average body weight.	Average radius of trachea.	Average area of tracheal cross-section.	$k = W^{0.71}/T$.	Tracheal cross-section as percentage of body-weight.	Cross-section calculated. $T = W^{0.71}/k$. ($k = 7{\cdot}44$.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (2·15) of body weight.	Difference between cross-section calculated and observed.
		grm.	mm.	sq. mm.				per cent.		per cent.
A	1–2	465	1·83	10·46	7·5	2·25	10·53	0·66	10·0	4·6
B	3–4	515	1·89	11·29	7·46	2·19	11·32	0·27	11·07	1·99
C	5–6	547	1·96	12·05	7·3	2·2	11·81	2·03	11·76	2·47
D	7–8	595	2·0	12·54	7·44	2·11	12·54	0·0	12·79	1·95
E	9–10	670	2·08	13·52	7·51	2·02	13·64	0·88	14·41	6·18
				Average	7·44	2·15	—	0·77	—	3·44

In Table VI the ptarmigan are arranged in five groups in the usual manner. In this case, as in that of the individual observations, the best n is 0·71, giving an average value for k of 7·44. The variations of the tracheal constant are without periodicity, but the tracheal percentage falls gradually, and quite regularly, from 2·25 to 2·02. Using the above values for n and k, the average deviation between the calculated and the observed figures is 0·77 per cent., while it is 3·44 per cent. (four and a-half times as great) if the area be calculated in per cent. of body weight. If the value of n be taken as 0·70, k becomes 6·98, and if n be 0·72, k is 6·93.

As regards the question of sex it is to be observed that, in the present series of observations, the average k for male animals is somewhat larger than average k for the females. That is to say, the *females* had slightly *wider* tracheas than the *males*.

In Table VII are tabulated the main results obtained, in such a manner as to show at a glance the range of weight, the best n, the value of k, the percentage deviation, and so forth, for each species of animal, both grouped and ungrouped. It will be seen from the averages brought out at the foot of the table that, taking the species together, the average percentage deviation for the individual animals between the calculated and the observed figures for the tracheal area is 9·02, when the calculation is made in terms of the body surface, while it is 14·23 when the area is expressed as a percentage of the body weight. The corresponding figures for the grouped animals are 2·5 and 12·28 respectively, a deviation nearly five times as large.

Just as was seen in our measurements of the aorta, the method used in measuring these tracheas is, in the nature of the case, much less exact than that employed by us in measuring the blood volume, and therefore gives much larger figures for the percentage deviation, yet this deviation is found to be reduced to very nearly the same extent in each case by grouping the animals; of course, reckoning by the body surface throughout. Thus, in the present instance, the ratio between individual and grouped percentage deviations is 9·02/2·5, *i.e.* 3·6, while in the other two cases it was shown to be 3·2.

The mean deviation between the calculated and the observed values, as determined by the method of least squares for the three species (grouped individuals), is 7·08 per cent. for the guinea-pigs, 1·58 per cent. for the rabbits, and 1·16 per cent. for the ptarmigan. The average of these figures is 3·27 per cent. The corresponding mean deviations when the tracheal area is calculated in percentage of body weight are for the guinea-pigs 33·42 per cent., for the rabbits 14·32 per cent., and for the ptarmigan 4·28 per cent., giving an average of 17·34 per cent.

Table VII.—Percentage Deviations, Constants, etc.

Animal.	Range of weight.	Weight of heaviest animal in terms of weight of lightest.	Best n.	k.			Average percentage deviation.				Deviation by weight divided by deviation by best n.
				$n = 0·70$.	$n = 0·71$.	$n = 0·72$.	$n = 0·70$.	$n = 0·71$.	$n = 0·72$.	As percentage of body weight.	
	grms.										
Guinea-pig :											
Individual	70–640	9·14	0·72	—	21·5	23·4	—	—	18·2	25·1	1·38
Grouped	70–630	9·0	0·71	20·1	21·3	22·5	—	5·46	5·76	22·49	4·12
Rabbit (tame) :											
Individual	940–2970	3·16	0·70	12·5	13·4	—	6·43	—	—	13·39	2·17
Grouped	955–2860	3·0	0·70	12·5	13·4	—	1·28	—	—	10·91	8·52
Ptarmigan :											
Individual	460–710	1·54	0·71	7·0	7·45	7·93	—	2·42	—	4·2	1·74
Grouped	465–670	1·44	0·71	6·98	7·44	7·93	—	0·77	—	3·44	4·47
Average percentage deviation taking best n { individuals							9·02			14·23	
Average percentage deviation taking best n { grouped							2·5			12·28	

The ratio between these figures (3·27 and 17·34) is also almost exactly the same as that which was found between the corresponding figures in the case of the blood volume (2), although in that case the mean deviations themselves were much smaller (namely, 1·39 and 7·82 per cent. respectively), owing to the much greater intrinsic accuracy of the technique.

From these figures it is seen that if a series of observations of the tracheal area are made and averaged, it follows that if the difference between this average and the theoretical value given by our formula is as much as **7** per cent. the tracheal area is probably abnormal, and if it amounted to about **10** per cent. it would be almost certain that the trachea was abnormally large or small. But if the measurements were expressed in percentage of body weight it would only be possible to say with the same degree of certainty that the tracheal area of the animal was abnormal when it differed from the calculated value by **50** per cent. or more.

The inter-relation of the various constants (for surface, blood, aorta, and trachea) given in the present and in previous papers, together with its significance, will be dealt with in a later communication. But it may here be pointed out that the value of n in the expression $W^n/a = k$ has now been shown to be 0·70–0·72 for the *surface area* of *three* different species of mammals, for the *blood volume* of *six* mammals, for the *aortic area* of *four* species of mammals and *four* species of birds, and for the *tracheal area* of *two* mammals and *one* bird. Accordingly we regard our formula $W^n/a = k$ as a rational formula indicating that the blood volume, the aortic area, and the tracheal area are all proportional to the body surface in warm-blooded animals. From an examination of the large number of data which we have now collected it appears that if one desires rapidly to compare a series of individual observations by means of the formula $W^n/a = k$, the value of k may readily be determined approximately by using the power $\frac{2}{3}$ (= 0·67) or the power $\frac{3}{4}$ (= 0·75) instead of the accurate value of n (0·70–0·72). The results thus obtained will be approximately correct over a moderate range of weight. But as the range of weight increases the results deviate from the true values, and those obtained with $n = \frac{2}{3}$ deviate more rapidly than those obtained with $n = \frac{3}{4}$.

The difference in the relative accuracy of the results given by these two values of n has been ascertained in the following manner:—The percentage deviations for the surface, the blood volume, the aortic area, and the tracheal area for four different species of animal, with " best n," with $n = \frac{2}{3}$, and with $n = \frac{3}{4}$, were tabulated, and the figures for these three values of n averaged. The final average deviations thus obtained were 2·52 per cent. with n taken as 0·70–0·72, 3·25 with n taken as $\frac{3}{4}$, and 3·81 with n taken as $\frac{2}{3}$. Thus

it appears that the value $\frac{3}{4}$ for n gives a deviation 1·29 times as great as that obtained with the best n, while if the value of n is taken as $\frac{2}{3}$ the deviation is 1·51 times as great as that with the best n.

Accordingly, it is clear that if an approximate value of n is employed for the sake of convenience in rapid calculation it is, as a rule, preferable to use the value $\frac{3}{4}$ rather than $\frac{2}{3}$. But wherever observations covering a wide range of weight are concerned it is essential to make use of the "best n" in order to obtain reliable results. In this connection it may be noted incidentally as a point of interest that the ratio between the deviations just quoted for $n = \frac{2}{3}$ and $n =$ best n, namely, 3·81/2·52 (*i.e.* 1·51), proves to be practically identical with the corresponding ratio already given elsewhere (2) in the case of the blood volume, namely, 2·08/1·39 (*i.e.* 1·5).

Conclusion.

Within a wide range of weight in any given species of warm-blooded animal the sectional area of the lumen of the trachea is proportional to the body surface, and can be calculated from the body weight by means of the formula $T = W^n/k$, where n has the value 0·70–0·72 and k is the constant to be ascertained for each particular species.

REFERENCES.

1. Dreyer, G., and Ray, W., 1910, "The Blood Volume of Mammals, as determined by Experiments upon Rabbits, Guinea-pigs, and Mice, and its Relationship to the Body Weight and to the Surface Area, expressed in a Formula," 'Phil. Trans.,' B, vol. 201, p. 133.
2. Dreyer, G., and Ray, W., 1911, "Further Experiments upon the Blood Volume of Mammals and its Relation to the Surface Area of the Body," 'Phil. Trans.,' B, vol. 202, p. 191.
3. Dreyer, G., Ray, W., and Walker, E. W. Ainley, 1912, "The Size of the Aorta in certain Animals and its Relation to their Body Weight," 'Journ. Physiol.,' vol. 44, p. xviii.
4. Dreyer, G., Ray, W., and Walker, E. W. Ainley, 1912, "The Size of the Aorta in Warm-blooded Animals and its Relationship to the Body Weight and to the Surface Area, expressed in a Formula," 'Roy. Soc. Proc.,' this vol., p. 39.
5. Dreyer, G., Ray, W., and Walker, E. W. Ainley, 1912, "The Relation between the Sectional Area of the Trachea and the Body Weight in certain Animals," 'Journ. Physiol.,' vol. 45, p. vii.
6. Meeh, K., 1879, "Oberflächenmessungen des menschlichen Körpers," 'Zeitschr. f. Biologie,' vol. 15, p. 425.